

# Upper Paleozoic biostromes in island–arc carbonates of the eastern Klamath terrane, California

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**Abstract.** The eastern Klamath terrane (eKt) of California, a geographically isolated, island–arc area, was invaded by biostromal communities during three intervals of carbonate deposition in the Carboniferous and Permian. Visean/Serpukhovian biostromes were formed on short-lived carbonate banks by the Tethyan brachiopod *Striatifera* and phylloid algae. Bashkirian biostromes on similar banks were formed by the cosmopolitan microproblematica *Tubiphytes* and *Donezella*. Wolfcampian biostromes occur in a thick carbonate platform and slope section and were formed by *Tubiphytes*, the phylloid alga *Eugonophyllum*, and *Palaeoaplysina*, an enigmatic taxon known mainly from Laurentia. Species diversity of biostrome dwellers increased from the Early Carboniferous to Early Permian, when it reached the level of high-diversity shelf–mud communities. Biostromes in the eKt record the global recovery of Carboniferous–Permian reef biotas during temporal intervals of quiescent volcanism that permitted carbonate deposition.

**Key words :** biostromes, California, Carboniferous, island–arcs, Permian

## Introduction

The Late Paleozoic, noted for its paucity of frame-building metazoans, was an interval of ecologic recovery of reef communities following their collapse in the Late Devonian extinctions (Sheehan, 1985 ; Copper, 1988). Island–arc carbonates of the eastern Klamath terrane, California (Figure 1), offer a picture of this recovery in a setting of geographic isolation, limited availability of favorable environments, and recurring biogeographic invasions from outside areas. Although no Late Paleozoic reefs or mound-like structures are known from the terrane, several reef-forming taxa are locally abundant in tabular limestone beds that represent biostromes. Biostrome formation was dominated by binding, baffling, and production of skeletal grains, and biostromal taxa included a mixture of algae, problematica and brachiopods (Figure 2).

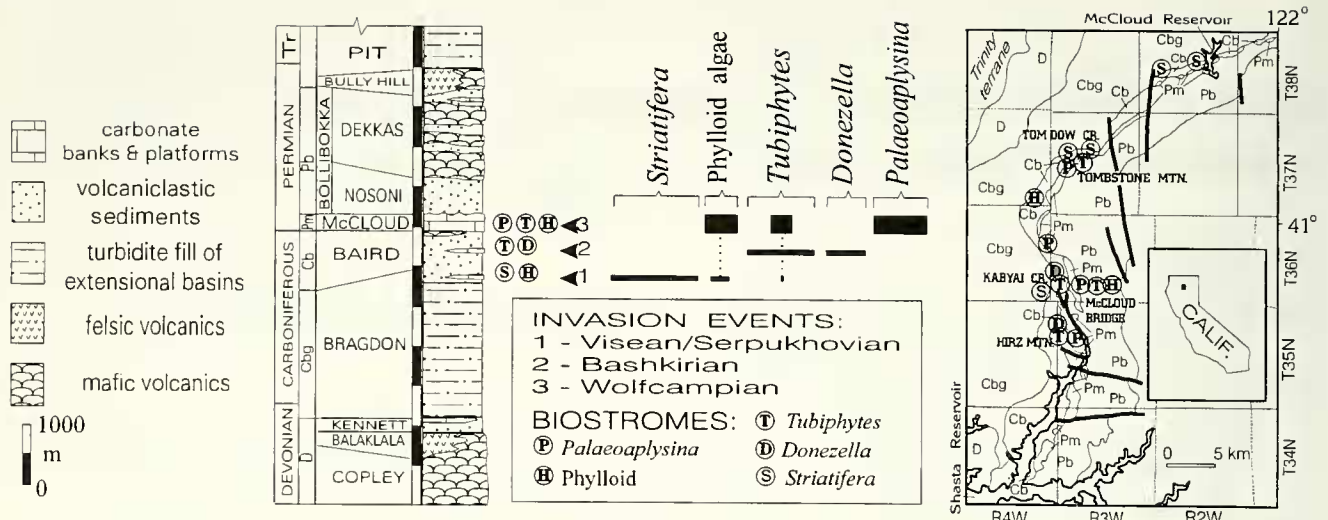
## Geologic setting

Devonian through Early Jurassic rocks of the eastern Klamath terrane (eKt) formed in a succession of island–arcs and arc-related basins (Albers and Bain, 1985 ; Renne and Scott, 1988 ; Miller, 1989). Renne and Scott (1988) summarized paleomagnetic data for the eKt, which indicate paleolatitudes equivalent to cratonic North America since at least Permian times. Paleozoic longitudinal position of the eKt with respect to North America has been a matter of debate. Miller (1987), Rubin *et al.* (1990), Miller and Saleeby (1991), Miller *et al.* (1992), and Darby *et al.* (1997) placed the

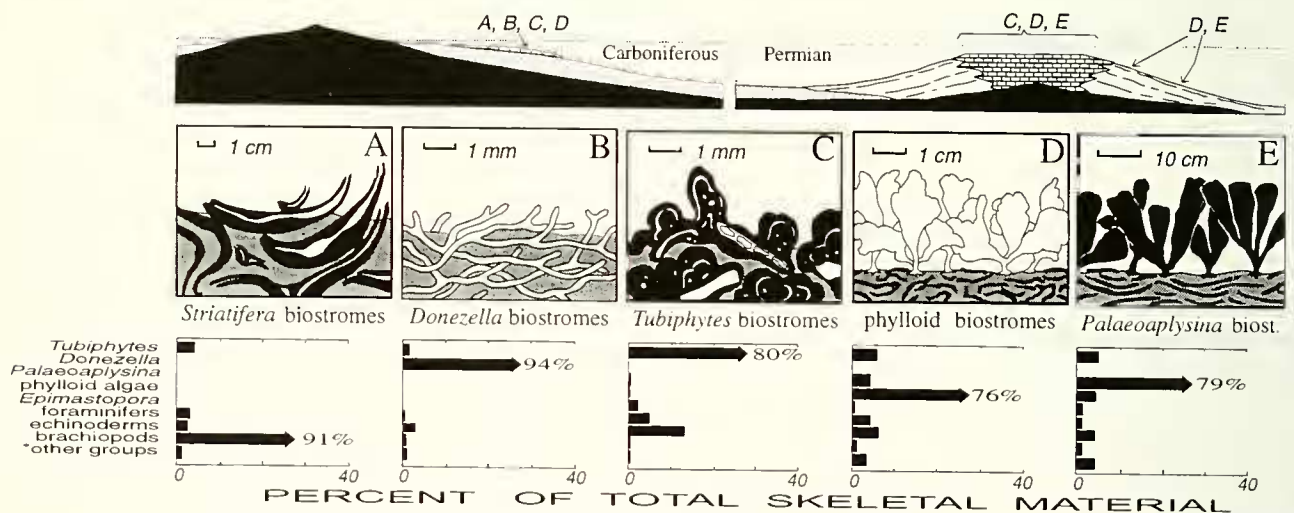
eKt near the western margin of cratonic North America, based on provenance of detrital zircons and stratigraphic ties with adjacent terranes. In contrast, Stevens *et al.* (1990) and Belasky and Runnegar (1994) concluded that the eKt formed in an oceanic setting thousands of km west of North America, based on Permian faunal composition and biogeographic models. In either scenario, the eKt represents an isolated area of shallow marine environments in the Paleozoic. Like a number of Cordilleran terranes (Soja, 1996), it contains a mixture of cosmopolitan, endemic, Tethyan and North American taxa (Watkins and Wilson, 1989 ; Watkins *et al.*, 1989 ; Potter *et al.*, 1990 ; Stevens *et al.*, 1990 ; Noble and Renne, 1990).

## Upper Paleozoic stratigraphy and carbonates

Early to Middle Devonian arc construction in the eKt was followed by extension and development of a large, arc-related basin in which submarine fan sequences of the Upper Devonian to Lower Carboniferous Bragdon Formation were deposited (Watkins, 1986, 1990 ; Miller and Cui, 1987 ; Miller and Saleeby, 1991). Volcaniclastic deltaic sediments with shallow marine limestone lenses appear locally at the top of the Bragdon and in the lower part of the overlying Baird Formation. The brachiopods *Striatifera* and *Titanaria* indicate a Visean or Serpukhovian (Late Mississippian) age for these limestones (Watkins, 1973 ; Gordon and Dutro, 1993). The lenses reach 17 m thick and 1.2 km in length, and consist of bank and slope facies that were deposited over delta lobes (Watkins, 1993a). Deposition of the lime-



**Figure 1.** Occurrence of Upper Paleozoic biostromes in the eastern Klamath terrane, California; width of bars for the five taxa indicates their relative importance in biostrome formation. Detailed geologic maps of areas with biostromes are contained in Watkins (1973, 1993a, 1993b).



**Figure 2.** Environmental occurrence, life habit reconstructions, and skeletal composition of biostromes (\*other groups include corals, bryozoans, annelids, molluscs, and ostracods).

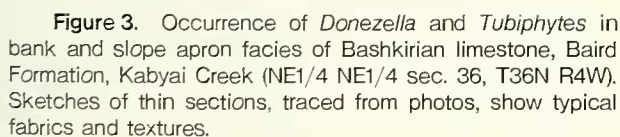
stone lenses was related either to sea-level rise that cut off volcaniclastic sediment supply, or to switching of active delta lobes. Carbonate deposition on deltas was short-lived and terminated by progradation of volcaniclastic sediments.

Bashkirian (Early Pennsylvanian) limestone lenses in the Baird Formation are dated by the fusulinid *Pseudostaffella* (Skinner and Wilde, 1965). The fusulinid-bearing limestones occur at Kabyai Creek (Watkins, 1973, fig. 4) and Hirz Mountain [the Hirz Mountain Limestone Member of Watkins (1973, fig. 3), who erroneously dated it as "Late Pennsylvanian or Early Permian"]. The lenses include bank and slope-apron facies (Figure 3), and they reach 20 m in thickness and 2 km in breadth. In both areas, the limestone lenses are

overlain by a thick section of volcaniclastic sediments that probably ranges from Bashkirian to latest Carboniferous age.

The Baird is overlain by the Lower Permian McCloud Limestone, which contains basal Wolfcampian to early Leonardian fusulinids (Skinner and Wilde, 1965). The McCloud was deposited during an interval of volcanic quiescence as several carbonate platforms that reached tens of km in breadth (Miller, 1989; Watkins, 1990). Platforms developed over volcanic highs and grew by progradation of slope deposits and aggradation of platform-top deposits, resulting in carbonate sections over 800 m thick (Watkins, 1993b). McCloud deposition was terminated by platform subsidence and drowning in the Leonardian, and volcanism





## Methods

Comparative paleoecology of biostrome and shelf-mud faunas, discussed later, uses the guild concept. Reef and biostrome guilds recognized by Fagerstrom (1987) include constructors, bafflers, binders, destroyers, and dwellers. This report follows Watkins (1993c) in subdividing the dweller guild on the basis of class-level taxonomy and functional morphology.

Biostromes formed by *Striatifera*, phylloid algae and *Palaeoaplysina* are readily apparent in the field, but their lateral extent is difficult to determine because of brush cover. *Striatifera* biostromes have been traced for lateral distances of 45 m, and *Palaeoaplysina* and phylloid biostromes have been traced for distances of 130 m. Biostromal beds dominated by *Donezella* and *Tubiphytes*, which appear as medium-grained, relatively featureless limestone in the field, were identified by thin sections. These beds have been traced only across small roadcuts and ledges.

*Striatifera* is a linoproductid brachiopod that attached to conspecific shells with its spines, forming biostromes similar to modern mussel beds (Muir-Wood and Cooper, 1960). An undescribed species of *Striatifera*, similar to *S. striata* Fischer de Waldheim, occurs as a biostrome former in Visean/Serpukhovian limestones of the Bragdon and Baird formations.

The biostromal beds range from 40 to 110 cm thick and contain a loose framework of in-place *Striatifera*. Articulated individuals rest upon one another in a convex-downward

orientation (Figure 4A) and are attached by cementing spines. Growth asymmetry caused by crowding is common, and shells range from juveniles a few mm in size to adults 18 cm in length. These beds contain 28 to 58% *Striatifera* and 33 to 59% micrite and microspar matrix. Small encrustations of *Tubiphytes* are present on *Striatifera* (Figure 5A) and form <1 to 14% of sediment volume. Other skeletal taxa are mainly matrix-supported and scattered between the large productoids; they form <1 to 10% of sediment volume and

include crinozoans, foraminifers, small brachiopods, gastropods, corals, echinoids, and bivalves (Watkins, 1973).

Beds with in-place productoids are interbedded with erosively based packstones that contain sorted, horizontally stratified *Striatifera* valves and fragments (Figure 4B). These two lithologies, which form horizons up to 3 m thick (Figure 4C), were deposited in a moderate to high energy, bank-edge setting (Watkins, 1993a).

### *Donezella* biostromes

Boundstone, packstone, and grainstone beds with abundant *Donezella lutugini* Maslov occur in Bashkirian limestones of the Baird Formation (Figure 3). Mamet (1991) placed *Donezella* and similar genera in the algal group Palaeosiphonocladales, but they have also been interpreted as sponges (Termier et al., 1977) and possible foraminifers (Riding, 1977). Mamet et al. (1987) interpreted the tubules of *Donezella* as branching thalli that stood upright above the bottom and functioned as sediment baffles. However, a sediment binding habit for donezellids is also possible (Davies and Nassichuck, 1988).

Massive beds from 35 to 120 cm thick contain 25 to 30% *Donezella* as an open-branching network of septate tubules 0.08 to 0.27 mm in diameter. The tubule network is partly contained in micrite (13–55% of sediment volume) and partly encloses spaces to 3.5 mm in size that consist of sparite (5 to 30%) and peloidal grainstone (14–25%). Fragments of echinoderms, bryozoans, foraminifers, and monaxial spicules occur in the micrite matrix, and areas of *Tubiphytes* up to 1.3 mm in size encrust *Donezella* tubules. These beds are interpreted as boundstone. Their texture and fabric are very similar to beresellid-donezellid boundstone in Bashkirian to early Moscovian reefs in the Canadian Arctic (Davies and Nassichuk, 1988).

Massive to cross-stratified beds of grainstone and packstone are 30 to 105 cm thick and contain 60 to 70% broken *Donezella* tubules (Figure 5C), 18 to 34% sparite or micrite matrix, and 1 to 8% other bioclasts, including *Komia*, *Tubiphytes*, echinoderms, foraminifers, bryozoans, brachiopods, and ostracods. Tubule fragments are 3 mm or less in length, and in some beds they show a parallel alignment of long axes. Other bioclasts, which reach 10 mm in size, are dispersed and often abraded. These beds represent sediment derived from *Donezella* boundstone, and they formed in moderate to high energy, bank and bank-edge settings.

### *Tubiphytes* biostromes

*Tubiphytes* is an encruster that has been interpreted as a cyanobacterium, alga, foraminifer, sponge, or metazoan of uncertain affinity (Riding and Guo, 1992). It consists of an outer envelope of dark, fine-grained calcite and internal tubules. Senowbari-Daryan and Flügel (1993) recognized only the envelope as *Tubiphytes* and considered the internal tubules as separate, overgrown organisms. Grainstones dominated by *Tubiphytes obscurus* Maslov occur in Bashkirian limestones of the Baird Formation and Wolfcampian zones A, B and G of the McCloud Limestone (Figures 3, 6).

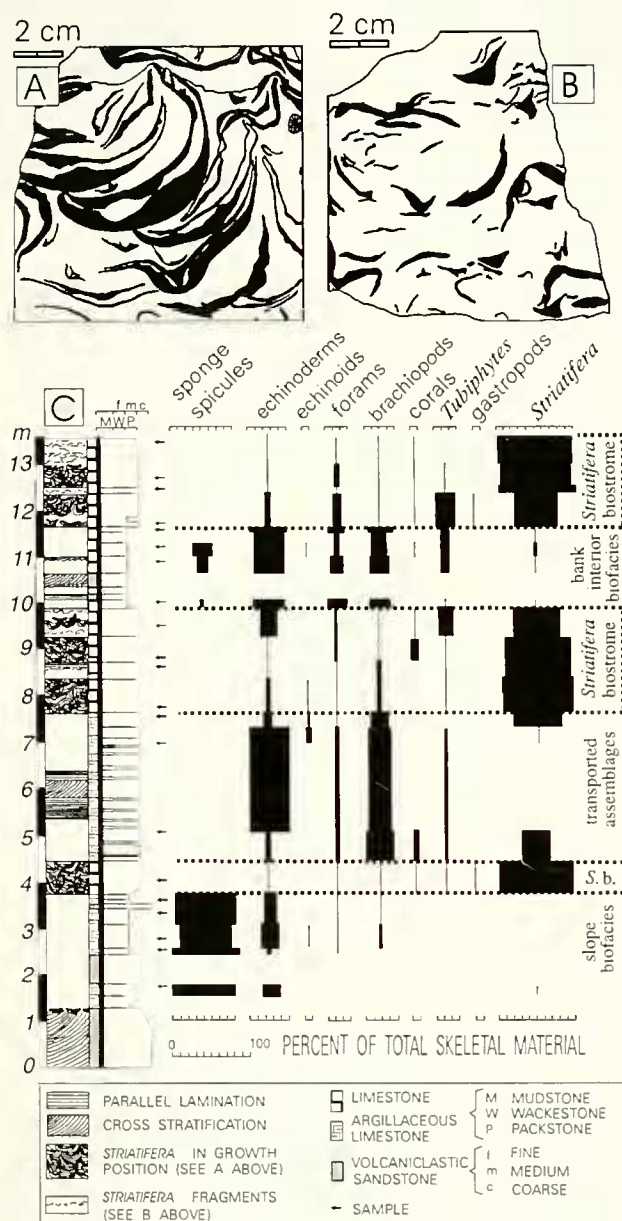


Figure 4. A. *Striatifera* in growth position. B. Rede-deposited *Striatifera* valves and fragments. C. Occurrence of *Striatifera* biostromes in limestone of the Baird Formation at Tom Dow Creek; see Watkins (1993a) for photos and location of this section.



In the bank facies of Bashkirian limestones, *Tubiphytes* grainstone forms massive to cross-stratified beds 30 to 140 cm thick. In the slope facies of these limestones, *Tubiphytes* grainstone and packstone form 10-to-30-cm-thick beds that include normal grading and small-scale cross-lamination (Figure 3). Wolfcampian *Tubiphytes* grainstone forms isolated, massive beds 0.4 to 5 m thick within platform successions of thick-bedded crinoid packstone, fusulinid packstone, and skeletal packstone (Figure 6). In Wolfcampian slope deposits at McCloud Bridge (fusulinid zone A of Skinner and Wilde, 1965), *Tubiphytes* grainstone is interbedded with limestone conglomerate and forms 10-to-60-cm-thick beds that include small-scale cross-lamination, horizontal lamination, and normal grading. At Tombstone Mountain, pebbles to small boulders of *Tubiphytes* grainstone are abundant in limestone conglomerates of fusulinid zone G.

The grainstones contain 43 to 80% *Tubiphytes* (Figure 5E) and 11 to 38% sparite to microspar matrix. *Tubiphytes* grains range from 0.3 to 1.5 mm, with a maximum size of 5 mm. Abrasion and rounding are common, particularly among smaller *Tubiphytes* grains that contain no other bioclasts. Larger *Tubiphytes* grains contain nuclei of small skeletal fragments or envelop and bind together several bioclasts. Other bioclasts, which include echinoderms, foraminifers, corals, bryozoans, brachiopods, and ostracods, reach 10 mm in size and form 1 to 19% of sediment volume. Permian beds also include the dasycladacean *Epimastopora* and indeterminate phylloid algae.

The grainstone beds indicate abundant *Tubiphytes* growth in shallow, high-energy settings where the volume of binders exceeded that of encrusted skeletal grains. Although small areas of *Tubiphytes* boundstone occur within skeletal packstone, no *Tubiphytes* bed with a complete boundstone fabric has been observed. This may indicate that *Tubiphytes* crusts were more or less continuously reworked as they formed. Kershaw (1994), in a classification of biostrome types, noted that not all biostromes consist of *in situ* skeletons. In Kershaw's classification, the *Tubiphytes* grainstone beds can be considered as "parabiostromes," which consist largely of reworked biostrome-formers, with 20% or less *in situ* material. Much of this sediment was also redeposited on slope aprons bordering bank and platform margins.

### Phylloid biostromes

Phylloid algae are a morphological group of leaf-like genera that may include both red and green algae (Riding and Guo, 1991). In Late Paleozoic reefs and biostromes, their functional role included sediment baffling and voluminous production of skeletal particles (Toomey and Babcock, 1983).

Phylloid packstone occurs as two 20-cm-thick beds in a single Visean/Serpukhovian limestone lens in the Baird Formation (Watkins, 1993a). Baird phylloids (Figure 5B) are recrystallized and generically indeterminate. In the Wolfcampian McCloud Limestone, phylloid packstone forms massive beds 0.3 to 4.5 m thick in platform successions (Figure 6). In McCloud slope deposits, gravity displaced

phylloid packstone occurs as clasts in limestone conglomerate and thin beds with erosional bases and normal grading. Slope deposits also include less common, massive beds to 80 cm thick that represent in-place biostromes. McCloud phylloids include *Eugonophyllum* sp., but specimens in most samples are too recrystallized for identification.

Packstones in the McCloud Limestone include 24 to 43% phylloids (Figure 5D) and 42 to 66% micrite and microspar matrix. Phylloid plates are 2 to 18 mm long, variably oriented, and closely to loosely packed. Edges of plates often appear broken but are unabraded. *Tubiphytes* forms <1 to 9% of sediment volume and occurs as loose grains and encrustations up to 4 mm long on phylloid plates. Spirorbids, fenestellid holdfasts, other bryozoans, and tetrataxiid foraminifers also encrust phylloids. Other bioclasts form 6 to 14% of sediment volume and are scattered, mostly matrix-supported, and mainly less than 5 mm in size. They include *Palaeoaplysina*, *Epimastopora*, bryozoans, foraminifers, echinoderms, gastropods, brachiopods, ostracods, and corals.

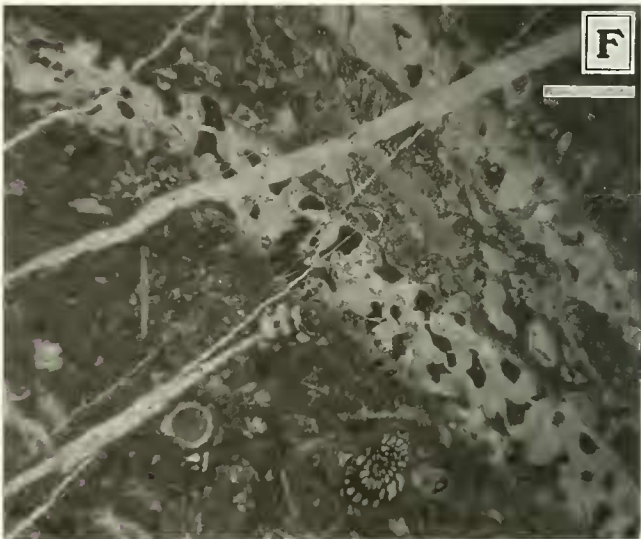
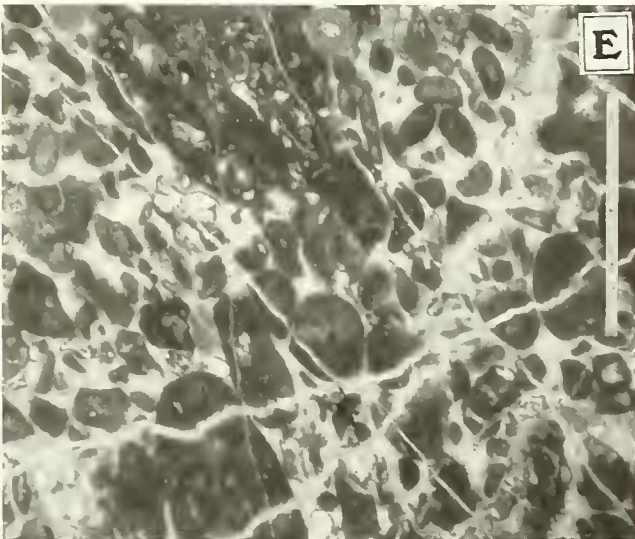
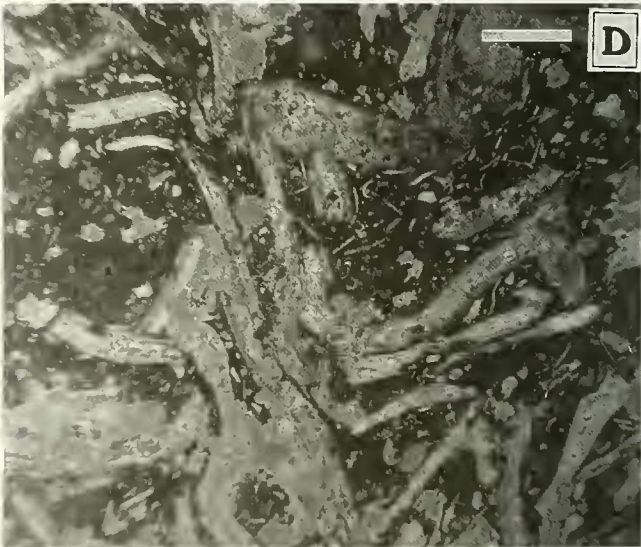
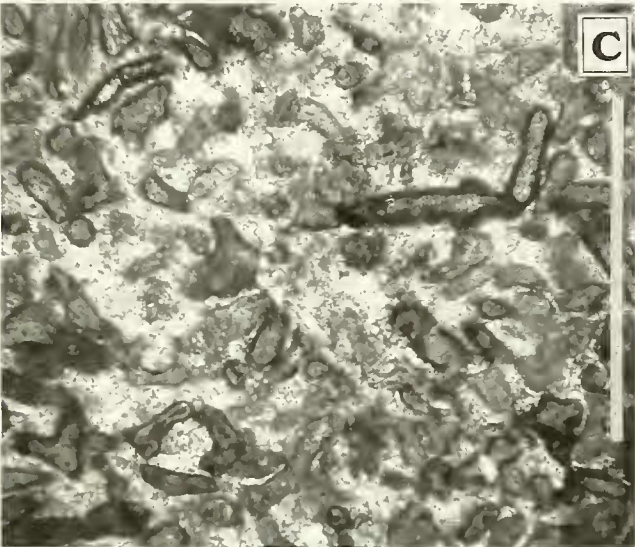
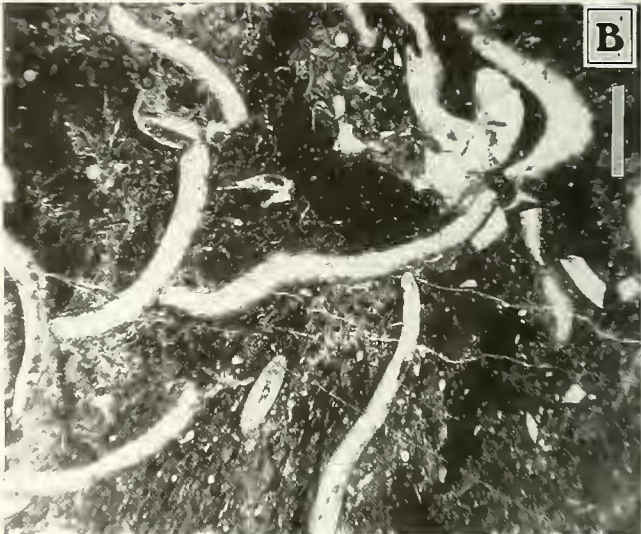
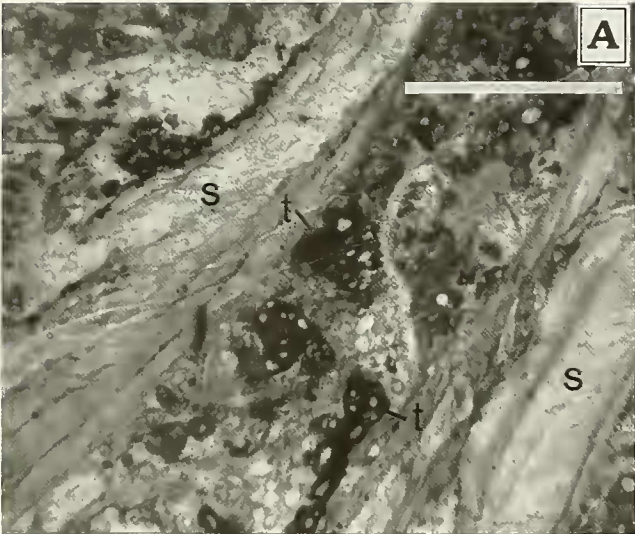
### *Palaeoaplysina* biostromes

The enigmatic genus *Palaeoaplysina*, which consists of thin calcareous plates with an internal canal system and cellular structure, has features in common with hydrozoans, sponges, and algae (Davies and Nassichuk, 1973). *Palaeoaplysina* is an important reef and biostrome former, but its mode of life is uncertain (Beauchamp et al., 1988). Breuninger (1976) inferred a binding habit for the plates, but Davies and Nassichuk (1973) and Watkins and Wilson (1989) presented evidence for an erect, frond-like growth habit.

*Palaeoaplysina laminaeformis* Krotov is locally common in the Wolfcampian McCloud Limestone (Figure 6). In the platform facies of the McCloud, massive beds of *Palaeoaplysina* wackestone to packstone are 0.7 to 2.2 m thick. These beds occur both as isolated units within successions of skeletal wackestones, packstones, and grainstones, and they are also interbedded with phylloid packstones as composite biostromal horizons over 4 m thick (Watkins and Wilson, 1989). McCloud slope deposits with limestone conglomerates also include common *Palaeoaplysina* beds (Watkins, 1993b). Massive *Palaeoaplysina* wackestone to packstone beds from 0.5 to 3 m thick are identical to those in the platform facies, and they are interpreted as in place biostromes of slope aprons. Less common, redeposited beds of *Palaeoaplysina* packstone are 10 to 30 cm thick and have loaded bases and ripple-laminated tops.

Beds of intergrading wackestone to packstone consist of 23 to 49% *Palaeoaplysina* (Figure 5F) and 38 to 69% micrite and microspar matrix. Plates of *Palaeoaplysina* reach 20 cm long, are mainly oriented parallel to bedding, and range from loosely to closely packed. Encrustors on *Palaeoaplysina* include *Tubiphytes*, which forms <1 to 4% of sediment volume, as well as spirorbids and bryozoans. Other bioclasts, which form 3 to 11% of sediment volume, include phylloid algae, *Epimastopora*, echinoderms, foraminifers, corals, bryozoans, brachiopods, gastropods, bivalves, and ostracods.





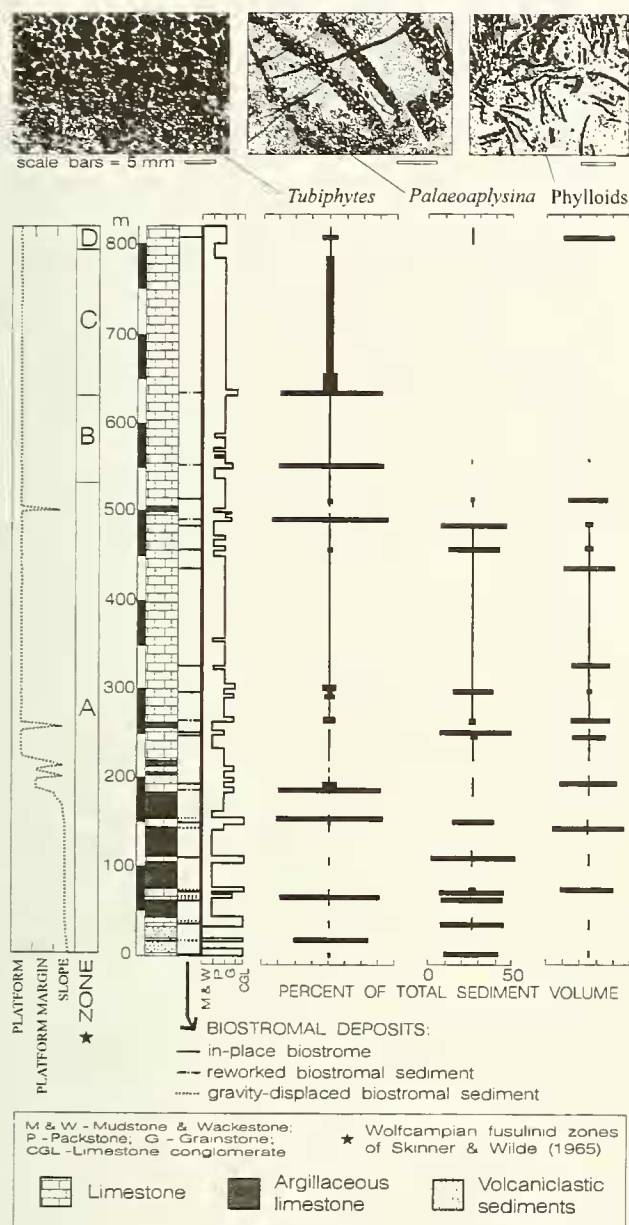


Figure 6. Biostrome occurrence in the Lower Permian McCloud Limestone at McCloud Bridge; see Watkins (1993b) for location, details of nonbiostromal lithologies, and bed-by-bed logs of parts of the section.

#### Biogeographic and sedimentary relations of biostrome formers

Three intervals of Late Paleozoic carbonate deposition in the eastern Klamath terrane were accompanied by bio-

strom formation. Biostromal taxa appear at or near the base of each carbonate horizon and range throughout their entire thicknesses; they have not been recorded through intervening clastic deposits. This suggests three separate invasions of the terrane by biostromal communities.

Biostromes were poorly developed during the Visean/Serpukhovian interval of carbonate deposition. The brachiopod *Striatifera* formed beds with a loose framework structure in several limestone lenses. However, *Striatifera* beds are not present in all lenses of this age (Watkins, 1993a), and their level of binding and sediment production was much less than those of other biostromes. *Striatifera* probably arrived in the eKt from the east, as it is a Tethyan genus that occurs in North Africa, Western Europe, Russia, Kazakhstan, China, and Japan (Muir-Wood and Cooper, 1960; Gordon and Dutro, 1993). Phylloid algae, which dominate two beds in one limestone lens, had only a limited role in sediment production, and their occurrence in the Baird Formation predates their Late Carboniferous rise as important producers of carbonate sediment (Chuvashov and Riding, 1984). The binder *Tubiphytes* is a minor constituent of the Visean/Serpukhovian biostromes, where its occurrence also predates its attainment of global abundance.

Bashkirian limestones of the eKt record the return of *Tubiphytes* and the appearance of *Donezella* as important biostrome formers. *Tubiphytes* grainstone forms up to 50% of the thickness of bank sections, and redeposited beds of *Tubiphytes* form up to 40% of sections deposited as slope aprons. The Bashkirian occurrence of *Tubiphytes* grainstones in the eKt corresponds to its rise in abundance during the Late Carboniferous, when it attained a cosmopolitan distribution as both a major and accessory reef and biostrome former (Chuvashov and Riding, 1984; Mamet, 1991; Senowbari-Daryan and Flugel, 1993). *Donezella* beds also form up to 50% of Bashkirian bank sections in the eKt. The Bashkirian/Moscovian was the temporal acme of *Donezella* as a sediment producer, and it forms reefs and biostromes of this age in North Africa, Eurasia, and North America (Mamet, 1991). Although phylloid algae were important and widely distributed reef and biostrome formers during the Late Carboniferous (Chuvashov and Riding, 1984; Mamet, 1991), they have not been observed in Bashkirian limestones of the Baird Formation.

Biostromes played a minor role in the construction of Wolfcampian carbonate platforms in the eKt. Beds dominated by *Tubiphytes*, phylloid algae and *Palaeoaplysina* form less than 10% of the thickness of platform sections. Lack of importance of biostromes and absence of reefs on McCloud platforms may be due to very high rates of subsidence and absence of well-defined platform margins (Watkins, 1993b). *Tubiphytes* and phylloids had a cosmopolitan distribution as important reef and biostrome formers in the Early Permian (Chuvashov and Riding, 1984; Riding and Guo, 1991; Senowbari-Daryan and Flugel, 1993). *Palaeo-*

Figure 5. A. Detail of *Striatifera* bed showing small encrustations of *Tubiphytes* (t) on *Striatifera* valves (s), Baird Formation, Tom Dow Creek. B. Phylloid packstone, Baird Formation, North Fork. C. *Donezella* grainstone, Baird Formation, Kabyai Creek. D. Phylloid packstone, McCloud Limestone, McCloud Bridge. E. *Tubiphytes* grainstone, McCloud Limestone, Tombstone Mountain. F. *Palaeoaplysina* packstone, McCloud Limestone, McCloud Bridge. All scale bars are 2 mm.



*aplysina* first appears in the Middle Pennsylvanian of Utah, and by the Wolfcampian it is present as a major reef and biostrome former in a belt around the northern margin of Laurentia, including occurrences in Idaho, British Columbia, the Canadian Arctic, Svalbard, and the Urals (Ritter and Morris, 1997). *Palaeoaplysina* is also known from the Akiyoshi terrane of Japan (Machiyama, 1991).

Early Permian *Palaeoaplysina* buildups appear to have had a relatively wide environmental range, occurring in the Canadian Arctic from inner shelf to upper slope settings (Beauchamp *et al.*, 1988). This relation is also evident in the McCloud Limestone, where *Palaeoaplysina* biostromes are present in both platform and slope deposits. McCloud slope deposits consist of alternations of thin-bedded argillaceous limestones and horizons with limestone conglomerates (Figure 6). *Palaeoaplysina* biostromes form 15 to 45% of the thickness of conglomeratic horizons. Occurrence of *Palaeoaplysina* biostromes on tops of conglomerates, as well as on volcanoclastic breccia at the very base of the McCloud Limestone (Watkins, 1993b, fig. 4), suggest a role as a pioneer community among carbonate sediment producers.

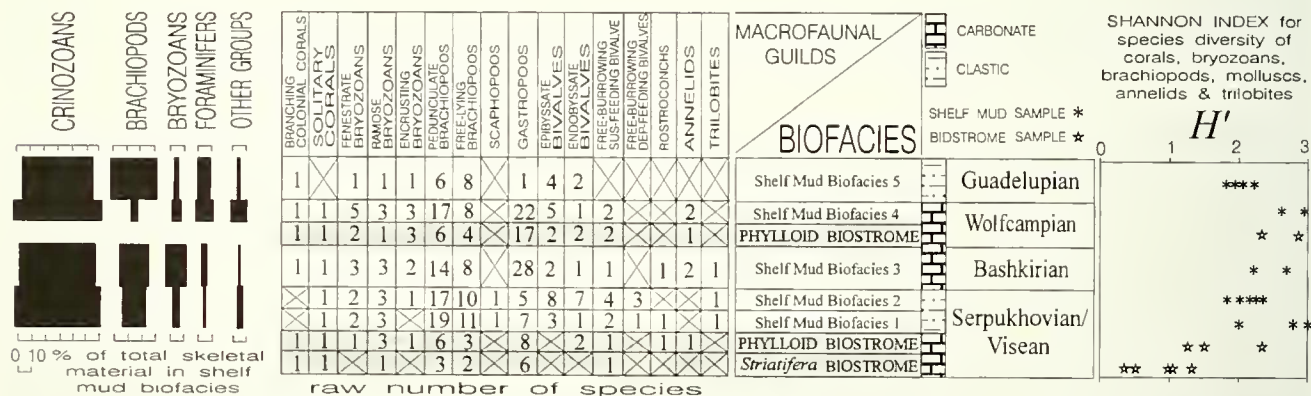
### Comparison of biostromes and shelf-mud biofacies

Paleoecological aspects of the biostromes can be best understood by comparison with contemporaneous shelf-mud biofacies of the eKt (Figure 7). The shelf biofacies occur in bioturbated, clastic and carbonate muds of Visean/Serpukhovian to early Guadalupian age (Coogan, 1960; Watkins, 1973; Yancey and Hanger, 1985). Echinoderms (mainly crinoids) form 50–70% of skeletal material in these biofacies, followed by brachiopods (4–36%), bryozoans (3–13%), foraminifers (1–11%), and molluscs, corals, and minor groups (<1–10%). Four bivalve guilds, three bryozoan guilds, two

brachiopod guilds, and a gastropod "superguild" include most of their macrofaunal species. Species data for echinoderms, which occur as disarticulated ossicles, are not available.

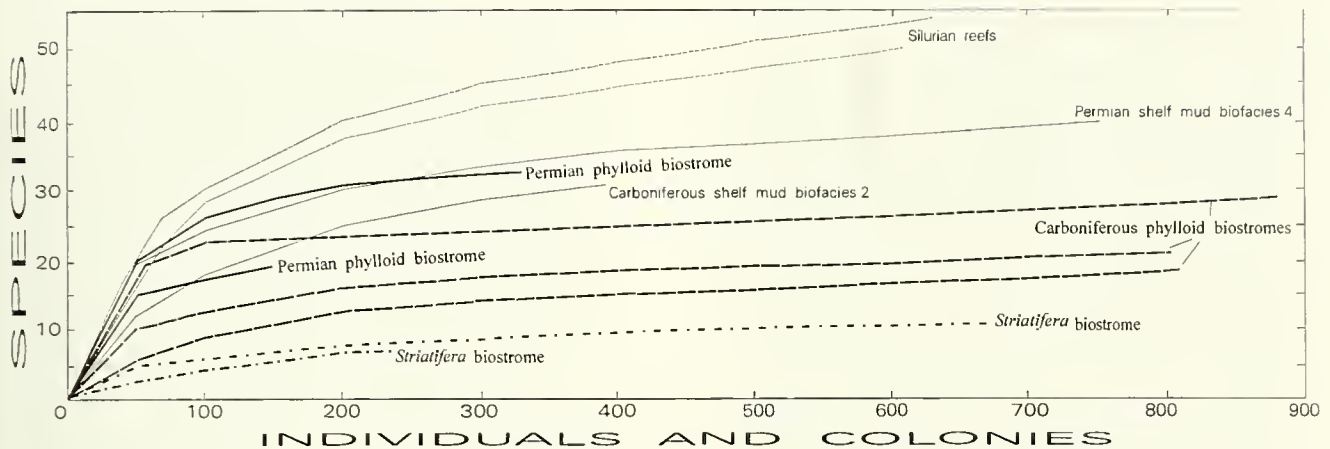
In contrast, all five types of biostromes are dominated by a single binding, baffling, or framebuilding species that forms over 70% of skeletal material (Figure 2). Although several such species may cooccur within a biostrome, only one predominates. For example, *Tubiphytes*, phylloids, and *Palaeoaplysina* commonly occur together in Lower Permian beds, but in each case one of these taxa is clearly dominant (Figure 6). Dweller guilds generally form 20% or less of skeletal material in beds, and their composition is similar in all five types of biostromes. Crinozoans and foraminifers are the most common dweller taxa (Figure 2), and small amounts of skeletal material (usually 2% or less each, except for *Striatifera* biostromes) are represented by brachiopods, bryozoans, molluscs, corals, annelids, and ostracods.

Bulk collections of silicified specimens from *Striatifera* and phylloid biostromes permit a more detailed consideration of dweller taxa (foraminifers, ostracods, and echinoderms have not been studied and are not included in this discussion or in plots of species diversity in Figures 7 and 8). The most diverse groups among dweller taxa are brachiopods and gastropods, followed in decreasing order by bryozoans, bivalves, corals, rostroconchs, and annelids. The composition and species diversity of dweller taxa in the biostromes is nearly identical to that in carbonate shelf-mud biofacies of Bashkirian and Wolfcampian age (Figure 7). In the Wolfcampian, the same species occur in shelf-mud biofacies, phylloid biostromes, and *Palaeoaplysina* biostromes (Watkins and Wilson, 1989). These relations suggest that most dweller taxa in the biostromes were not specialized for these habitats, but were immigrants from level bottom, carbonate



**Figure 7.** Faunal comparison of Upper Paleozoic biostromes and shelf-mud biofacies of the eastern Klamath terrane. Biofacies are arranged vertically by four intervals of time, but this plot is not a stratigraphic section. For the Serpukhovian/Visean, relative stratigraphic position of phylloid and *Striatifera* biostromes is not known, and both overlap in stratigraphic range with shelf-mud biofacies. For the Wolfcampian, plotting of the phylloid biostrome below the shelf-mud biofacies is arbitrary, as these biotas are interbedded. Shelf-mud biofacies and number of specimens in samples (*n*) are as follows: 1-*Dorsoscyphus* association, Bragdon Formation, *n*=442; 2-*Rugosochonetes* association, Baird Formation, *n*=1203; 3-*Lissomarginifera* association, Hirz Mountain Limestone Member of Baird Formation, *n*=1734; 4-*Crurithyris* (= *Cruricella*) association, McCloud Limestone, *n*=1663; 5-*Anidanthus-Spiriferella* faunule, *n*=435. Sample sizes for biostromes are as follows: Wolfcampian phylloid, *n*=472; Serpukhovian/Visean phylloid, *n*=2496; *Striatifera*, *n*=1261.





**Figure 8.** Rarefaction curves for Upper Paleozoic biostromes and shelf-mud biofacies of the eastern Klamath terrane. Also shown for comparison are two samples from Silurian reefs (Watkins, 1996). Data are for corals, bryozoans, brachiopods, molluscs, annelids and trilobites.

mud environments.

#### Trends in species diversity

Following the Late Devonian extinctions, the global number of marine families increased rapidly, reaching a stable level near the end of the Early Carboniferous that was maintained for the rest of the Paleozoic (Sepkoski, 1992). This pattern of Late Paleozoic stasis is also shown by species diversity of Visean/Serpukhovian to early Guadalupian shelf-mud biofacies of the eKt, as measured by  $H'$  and rarefaction (Figures 7, 8). Reef biotas were much slower to recover from the Late Devonian extinctions, and complex reef communities were not reestablished until the Middle Permian (Sheehan, 1985; Copper, 1988). This slow recovery is also suggested by species diversity data from Upper Paleozoic biostromes in the eKt. Average species-diversity in eKt Carboniferous biostromes is less than that of shelf-mud biofacies. Species diversity in phylloid biostromes increased by the Early Permian, when they attained a diversity equivalent to that of carbonate shelf-mud biofacies (Figures 7, 8). Even so, diversity of the Early Permian biostromes did not reach the levels of reefs that existed before the Late Devonian extinctions, as shown by rarefaction curves for Silurian reefs (Figure 8).

#### Conclusions

Three intervals of Late Paleozoic volcanic quiescence and carbonate deposition in the eastern Klamath terrane were accompanied by development of biostromal communities. Except for loosely cemented productoid brachiopods, framebuilders are absent, and bafflers and binders of algal or problematic affinity are the dominant biostrome formers. Stratigraphic ranges and peaks in abundance of eKt biostromal taxa are like their occurrences elsewhere. Biostrome formers include a mixture of cosmopolitan, Tethyan and Laurentian affinities. An increase in species diversity from

Early Carboniferous to Early Permian biostromes in the eKt probably reflects global recovery of reef biotas following the Late Devonian extinctions.

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